Latitudinal Variation in Parasitoid Guild Composition and Parasitism Rates of North American Hawthorn Infesting *Rhagoletis*

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ABSTRACT *Rhagoletis pomonella* (Diptera: Tephritidae) populations in North America have diverged by exploiting host plants with varying fruiting phenologies in environments that differ markedly in temperature and humidity. As a result, four genetically and ecologically distinct *R. pomonella* populations that display partial reproductive isolation have evolved. Host shifting by *Rhagoletis* and similar evolutionary histories could have had cascading effects across trophic levels, influencing the diversity and distribution of associated parasitoid guilds. To establish the basis for a future understanding of the possible effect of divergence in *R. pomonella* populations on the parasitoids attacking these flies, we surveyed parasitoids from five different species of hawthorns distributed over 15 states in México and 2 states in the midwestern United States. Emerging parasitoids were identified, parasitism rates were calculated, and regional fly and parasitoid emergence schedules were determined. Parasitism rate, emergence schedules, Shannon-Weiner diversity indexes, and species accumulation curves were compared across three main geographical regions. Parasitism levels varied greatly among regions from an overall high of 27.2% in the United States to 5.5% in the Sierra Madre Oriental (SMO) mountains of Mexico, to as low as 0.19% in the Eje Volcánico Trans Mexicano (EVTM). Shannon-Weiner diversity indexes showed that parasitoid species diversity was similar across the distribution range of *R. pomonella* in Mexico and the United States because of the fact that total parasitism was dominated by only two species, one of them recovered across the whole North American range of hawthorn infesting *Rhagoletis*. Nevertheless, eight parasitoids were found attacking *R. pomonella* in Mexico compared with only four collected in the United States. Only two diapausing parasitoid species were shared between the U.S. and Mexican *R. pomonella* populations: *Utetes canaliculatus* and *Diachasmimorpha mellea*. Interestingly, many subtropical parasitoid species, usually associated to flies in the subtropical genus *Anastrepha*, were recovered in the SMO in low numbers. The wide distribution of *U. canaliculatus* and *D. mellea* offers an ideal opportunity to test for a shared biogeography and co-evolution between fly and parasitoids. In this regard, one factor contributing to the success of *U. canaliculatus* seems to be the wasp's ability to modulate its eclosion time to track regional variation in hawthorn fruiting phenology and host (i.e., fly larvae) availability. Both *R. pomonella* and *U. canaliculatus* from southern sites emerged later than insects from northern populations, mirroring seasonal differences in hawthorn fruiting times across Mexico and the United States. These results suggest that molecular studies and crossing experiments could show, as they have for *Rhagoletis*, recent speciation events for parasitoid species of Nearctic origin that were found to be ecologically tracking environmentally driven divergence of their tephritid hosts.

KEY WORDS Braconidae, co-evolution, North America, *Rhagoletis pomonella*, Tephritidae

Understanding spatial and temporal patterns of species diversity and abundance are major goals of ecology (Gaston 2000, Witman et al. 2004). Because herbivorous insect specialists are the most numerous group of animals on earth, considerable attention has been focused in trying to accurately estimate phytophagous insect diversity in nature and understanding the underlying mechanisms behind the observed diversity/distribution patterns (Erwin 1997, Godfray et al. 1999, Basset 2001). Many monophagous/stenophagous insects (i.e., exhibiting close associations with one or a reduced number of hosts (Aluja and Mangan 2008) are severely attacked by natural enemies, particularly guilds of hymenopteran wasps (Stireman et al. 2006). It has been suggested that the same factors that affect phytophagous insect diversity often influence the radiation of their associated natural enemies

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Fig. 1. Map of collecting sites in the United States and Mexico. Gray dots represent collection sites where flies but no parasitoids were recovered; black dots represent sites where flies and parasitoids were found. The natural range of *R. pomonella* in the United States is delineated by dashed black lines, in the Sierra Madre Oriental (SMO) by a solid gray line, and in the Eje Volcánico Trans Mexicano (EVTM) by a black doted line.

(Bernays and Graham 1988, Abrahamson et al. 2003, Smith et al. 2006, Stireman et al. 2006). If this is true, host-specific parasitoids may constitute a generally underestimated and underappreciated component of global biodiversity. Moreover, discerning how parasitoid assemblages co-evolve with their herbivorous hosts would be of fundamental importance for understanding insect community ecology and structure (Stireman and Singer 2003).

The apple maggot fly, *Rhagoletis pomonella* (Walsh), is a classic example of incipient sympatric speciation through host plant shifts (Berlocher and Feder 2002). Sympatric divergence has been hypothesized to have occurred not only between hawthorn (*Crataegus* spp.) and apple (*Malus pumila*) host races of *R. pomonella* (Bush 1966, Feder et al. 1988, McPheron et al. 1988) but also among several sister species throughout the *pomonella* group (Berlocher 2000). Recent genetic studies of Mexican hawthorn-infesting populations of *R. pomonella* (Feder et al. 2003, 2005; Michel et al. 2007; Xie et al. 2007, 2008) have shown that U.S. and Mexican flies share a complicated history of isolation, contact, and differential introgression that may have played a role in facilitating sympatric host shifts in the United States (details follow). Here, we survey the abundance and distribution of *R. pomonella*'s associated braconid parasitoids in Mexico and midwestern United States as a first step toward analyzing the potential for co-evolution and a shared biogeography between flies and wasps.

Rhagoletis pomonella infest various species of native hawthorns throughout much of the range of *Crataegus* in Mexico (Rull et al. 2006). Two geographically isolated and genetically differentiated populations of *R. pomonella* or near *pomonella* have been recently identified in Mexico (Rull et al. 2006, Xie et al. 2007). One

population of flies infests late (October–January) fruiting species of hawthorns across the highlands of the Eje Volcánico Trans Mexicano (EVTM; Fig. 1; Table 1). The second population occurs through the Sierra Madre Oriental (SMO) mountains and infests relatively early (July–October) fruiting species of hawthorns (Rull et al. 2006, Xie et al. 2007). Genetic data imply that the two populations were initially isolated ≈1.57 Mya (Feder et al. 2003, 2005; Xie et al. 2007). However, there seems to have been repeated episodes of contact between the EVTM and SMO fly populations that introduced diapause life history variation into the SMO population in the form of inversion polymorphism. A recent study using microsatellites (Michel et al. 2007) has suggested that the Mexican SMO population may not be completely isolated from the current U.S. hawthorn fly population and that the SMO has served as a conduit for gene flow in the past enabling the inversions to reach the United States and Canada. Apparently the inversions served as an important source of phenological variation facilitating the radiation of U.S. flies onto a number of new hosts (e.g., apples) with differing fruiting phenologies, helping spawn the *R. pomonella* complex (Feder et al. 2003, 2005; Xie et al. 2007, 2008).

The complex history of the *R. pomonella* group begs the question of whether, and to what degree, the evolution of its associated parasitic wasps has been shaped by similar geographic and ecological factors. In this regard, previous work has documented that a number of egg-prepupal, larval-prepupal, and pupal hymenopterous parasitoid species attack the apple maggot fly North of Mexico, including the braconids *Diachasmimorpha mellea* (Gahan) [synonymous with *Biosteres melleus* (Gahan)], *Opius downesi* (Gahan), *Utetes lectoides* (Gahan) (=*O. lectoides* Gahan), *U.*

Table 1. Geographical location of sites where fly-infested hawthorn was collected

State	Locality	Coordinates (lat. N/long. W)
Michigan	Grant	43.20/85.48
	Casnovia	43.09/85.44
	Fennville	42.35/86.06
Indiana	Granger	41.07/86.14
	South Bend	41.67/86.25
Chiapas	Huixtán	16.43/92.27
	Rancho Nuevo	16.42/92.37
	Teopisca	16.32/92.28
	San Cristóbal de las Casas	16.45/92.38
Coahuila	El Tejocote	25.17/101.37
Distrito Federal	Tlálpan	19.17/99.10
Guerrero	Peral Tetipac	18.35/99.37
Hidalgo	Acoalitlán	20.47/98.43
	Achocoatlán	20.46/98.43
	Atotonilco	20.15/98.38
	Durango	20.53/99.13
	Duraznos	20.51/99.14
	Ixmiquilpan	20.39/99.14
	La Mora	20.59/99.04
	La Pechuga	20.40/99.14
	Minas Viejas	20.55/99.12
	Mojonera	20.37/98.36
	Zoquiazoquitlán	20.38/98.43
Jalisco	Atemajac de Brizuela	20.11/103.43
	Los García	19.38/103.39
	Mazamitla	19.54/103.03
	Tapalpa	19.57/103.47
México	Atlacomulco	19.49/99.54
	Carretera a Zitácuaro	19.17/100.07
	Texcoco	19.30/98.53
	Toluca	19.24/99.42
	Valle de Bravo	19.03/100.00
Michoacán	Angangueo	19.36/100.18
	Ciudad Hidalgo	19.41/100.37
	La Dieta	19.26/100.12
	Mil Cumbres	19.37/100.46
	Tancítaro	19.20/102.22
	Uruapan	19.28/102.03
	Villa Morelos	20.00/101.23
Morelos	Coajomulco	19.03/99.11
	Tres Marías	19.01/99.16
Nuevo Leon	Cerro el Potosí	24.52/100.11
	El Orito	24.55/100.12
	Santiago	25.25/100.09
Puebla	Chingnahuapan	19.43/98.04
	Miradores	19.50/97.30
	Poxcuatzingo	19.58/97.57
	San Martin Zacatempan	18.53/98.36
	Xoxonocaxtla	20.00/97.56
Querétaro	San Joaquín	20.55/99.34
	Santa Ana	20.54/99.32
San Luis Potosi	San Francisco	21.57/99.50
	Valle de los Fantasmas	21.56/99.56
	Carretera a Rio Verde	22.00/100.08
Tlaxcala	Xaltocan	19.25/98.12
Veracruz	El Rosario	19.35/96.58
	La Joya	19.38/97.05
	Las Vigas	19.38/97.06
	Piletas	19.35/96.56
	Rafael Lucio	19.36/96.57
	Xalapa	19.32/96.55

canaliculatus (Gahan) (=*O. lectus* Gahan), *Diachasma alloeum* (Muesebeck) (=*O. alloeus*), and *D. ferrugineum* (Gahan) (Rivard 1967, Monteith 1971, 1977, Dean and Chapman 1973, Cameron and Morrison 1977, Maier 1981, AliNiazee 1985, Gut and Brunner 1994, Feder 1995). In addition to the braconids, the parasitoids *Pteromalus* sp. (Pteromalidae), *Tetrastichus* spp. (Eulophidae) (Gut and Brunner 1994), *Psilus* sp. (Diapriidae) (Cameron and Morrison 1974) have also been recorded attacking *R. pomonella* in the United States. Parasitism levels in the United States have been shown to vary greatly depending on host plant species. For example, overall parasitism rates range from 0 to 23% for flies infesting apple compared with 7.9–90% on different species of hawthorns (Maier 1981, Gut and Brunner 1994, Feder 1995). Escape from parasitism in apples ("enemy free space"; Hairston et al. 1960, Jeffries and Lawton 1984) may have contributed to sympatric host race formation for *Rhagoletis* by compensating for initially poorer physiological performance of larvae feeding in a novel fruit (Feder 1995). Notably, the emergence schedules of *Diachasma alloeum* populations seem to be synchronized with that of its host, *R. pomonella* flies, infesting earlier fruiting apples. In the United States, hawthorns invariably fruit later than apples and the two *R. pomonella* host races have adapted to the fruiting phenologies of their hosts (Feder 1995). Such host-related differentiation by the frugivorous fly can potentially lead to parallel diversification in its parasitoids (Stireman et al. 2006) through concomitant effects that cascade across trophic levels.

Our previous work on *Rhagoletis* and its nearctic parasitoids has highlighted the potential for ecological factors to facilitate cascading host-associated differentiation (Feder 1995). However, the question of the role that biogeography may have played in the coevolution of the fly, and its associated parasitoids, has not been explored, and no prediction on subtropical parasitoid species exploiting *R. pomonella* in areas of overlap in Mexico can be accurately made with existing information. Therefore, here, we begin to address this issue through a survey of the diversity and relative abundance of hymenopteran parasitoids attacking Mexican hawthorn fly populations in the EVTM, the SMO, and two Midwestern states in the United States in an effort to link our knowledge of host associated differentiation in the northern range of *R. pomonella* with the biology of southern populations.

Materials and Methods

Study Sites, Sample Collection, and Processing Procedures. Egg and larval-infested hawthorn (*Crataegus spp.*) fruit were collected from a total of 62 sites spanning 15 different states in Mexico and 2 states in the United States during the 2001 through 2005 field seasons. The 62 sites included 24 locations in the EVTM, 30 in the SMO, 3 in Chiapas (Sierra de los Altos de Chiapas), and 5 in the United States (Fig. 1). The highlands of Chiapas represent a geographically isolated hawthorn fly population south of the SMO (Fig. 1). Five different infested hawthorn sites were sampled in the United States from Grant, MI, Casnovia, MI, Fennville, MI, Granger, IN, and South Bend, IN. Detailed information concerning the collecting sites and dates are given in Table 1.

Infested hawthorn fruit ($\approx$95% collected from ground and 5% picked in tree canopies) were transported back to the laboratory at the Instituto de Ecología, A.C. in Xalapa, Veracruz, and kept on plastic perforated racks positioned over plastic trays. Emerging fly larvae leaving host fruit and forming puparia were collected on a daily basis from the trays. The pupae were transferred to small (200 ml) plastic containers with moist vermiculite and kept in a room at ambient environmental conditions until fly or wasp emergence. Numbers of newly emerging flies and adult parasitoids were recorded for all sites on a daily basis throughout the emergence period (ranging from 5 to 7 mo). Adult parasitoids were kept for 2–3 d on a honey and water diet to allow full pigmentation and sclerotization to occur and were stored in 70% alcohol before identification.

Determination of Parasitism Rates. Parasitism rates (i.e., percent parasitism) were calculated by dividing the total number of emerged parasitoids over the sum of emerged parasitoids and flies. We note that estimating parasitism rates for *R. pomonella* was complicated by the fact that certain wasps are parasitoids of second- and third-instar fly larvae and oviposit into both fallen and unabscised fruit. As a result, estimates derived from field-collected fruit can underestimate parasitism rates for larval stage parasitoids because host flies in fruit are not exposed to these wasps for the full duration of time that they would normally be in nature. It is difficult to predict a priori how great this underestimation may be. As a consequence, parasitism levels reported in this study for wasps that attack fly larvae in abscised fruit should be considered as lower-bound estimates of rates in the field. However, considering the consistent nature of our sampling scheme (i.e., combination of 5% picked and 95% abscised fruit collected from ground at all sites), the magnitude of the slight underestimation was likely uniform across locations.

We also took precautions to avoid underestimating parasitism levels caused by uneclosed pupae. It is not uncommon to find that up to 50% of the pupae derived from field-infested fruit and reared in the laboratory fail to eclose after winter diapause. On the one hand, this mortality can be caused by natural attrition (exhaustion of energy reserves before emergence) of flies. On the other, it is also possible that a disproportionate number of these deaths could be caused by successful parasitism leading to unsuccessful life cycle completion. That is, many times the parasitoids fail to complete development and emerge for a variety of reasons. To obtain an accurate estimate of the mortality caused by parasitism in cases where no parasitoid or fly emerged from a puparium, we dissected between 20 and 63 uneclosed pupal cases per collecting site (sample size tied to availability of pupae at each collecting site), from two SMO sites (La Mora, LA Pechuga), two EVTM sites (La Dieta, Toluca), one Chiapas site (Huixtán), and the Grant, MI, site. Dissections were made by cutting the puparium open with a scalpel and removing the pupal case with a pair of tweezers to show its interior. Parasitoids can be easily distinguished from flies in a dissected puparium on account of their long beaded antennae. Dissection of puparia showed that mortality caused by parasitism was similar when comparing the proportion of nonemerged flies because of parasitism (i.e., as ascertained by dissections) with percent parasitism determined by direct counts of emerged flies and parasitoids. Moreover, the pattern of heavy parasitism in the United States, moderate levels in the SMO, and rarity in the EVTM and Chiapas highlands was closely mirrored in estimates based on dissected pupae. Consequently, there was no consistent underestimate of parasitism in the study caused by increased mortality in noneclosed pupae.

Determination of Parasitoid Emergence Schedules. To determine whether the life histories of parasitoids mirror the north–south latitudinal cline of increasingly later emergence time observed for hawthorn flies from the United States and Mexico (Feder et al. 2003, Xie et al. 2007), emergence curves were determined for flies and wasps reared under controlled and standardized environmental conditions for a subset of EVTM (Distrito Federal), SMO (Ixmiquilpan), and U.S. (South Bend) sites. For the emergence studies, infested hawthorns were collected from the field and handled as described above. However, 2 wk after pupation, instead of keeping pupae at ambient temperature, they were placed in a refrigerator at 5°C for 14 wk to simulate winter. After removal from the refrigerator, pupae were held in an incubator at 23°C, and emergence dates for adult flies and parasitoids were recorded daily.

Taxonomic Identification and Placement of Voucher Specimens. All parasitoids were identified by two of us (L.G. and R.A.W.). Voucher specimens have been placed in the permanent insect collection at the University of Texas A & M (TAMU) in College Station, TX. Additional voucher specimens have been placed in the permanent insect collection of the Instituto de Ecología, A.C. (INECOL) in Xalapa, Veracruz, Mexico (INEXAL). Identification of hawthorn specimens was performed by J.R. with the assistance of Claudia Gallardo at the IXAL herbarium using the taxonomic keys of Phipps (1997). Voucher specimens have been placed in the permanent plant collection of the INECOL in Xalapa, Veracruz, Mexico (IXAL).

Data Analysis. Regional (U.S., SMO, EVTM) parasitism rates were compared among fly populations with a linear model (GLIM) followed by analysis of variance (ANOVA) using Statistica. Diapause length for (1) flies and (2) the parasitoid *Utetes canaliculatus* from three regions (U.S., SMO, EVTM) was compared by means of linear models (GLIM) followed by ANOVAs using Statistica. Shannon-Weiner diversity indexes were calculated for each sample, in each geographical region by applying the formula $e^{-\Sigma p_i \times \ln p_i}$ (where p_i = proportion of species i, and $\ln p_i$ is the natural log) and compared by means of a linear model (GLIM) followed by ANOVA using Statistica. Rarefaction curves were constructed for each region using EstimateS (http://purl.oclc.org/estimates). To increase sample size, six samples of infested hawthorn
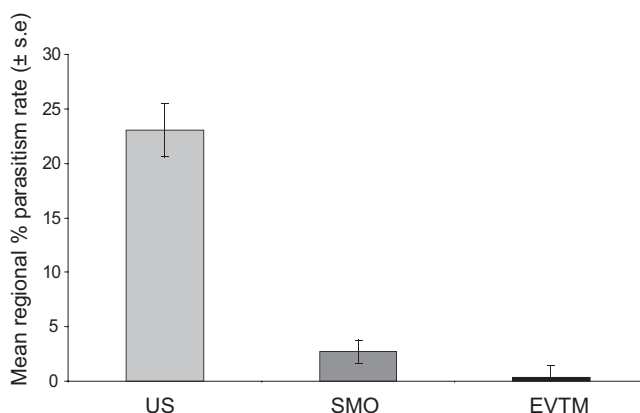
Fig. 2. Mean percent (±SE) regional parasitism rate for U.S. (light gray bar), SMO (gray bar), and EVTM (black bar) populations of *R. pomonella.*

from Connecticut (Maier 1981) were incorporated into the database to build species accumulation curves for the United States.

Results

Parasitism Rates. ANOVA showed highly significant differences in parasitism rates for fly populations from the three regions under analysis (U.S., SMO, EVTM; $F_{2,59} = 35,727$; $P < 0.00001$; Fig. 2). Parasitism rates were significantly higher for hawthorn flies from the five U.S. populations collected from Grant, MI, Casnovia, MI, Fennville, MI, Granger, IN, and South Bend, IN (Table 2). A total of 1,410 flies and 526 adult parasitoids eclosed from ≈2,500 *R. pomonella* pupae recovered from infested *C. mollis* at the five U.S. sites, resulting in an overall parasitism rate of 27.2% (=526/1,410 + 526). Parasitism rates varied among sites from a high of 42.8% for the Fennville, MI, site to a low of 5.1% for the Granger, IN site (mean rate across U.S. populations = 23 ± 13.5% SD). There was a trend for higher parasitism at the three more northern sites in Michigan (21.9, 33.3, and 42.8%) than at the two sites in Indiana (5.1 and 12.3%). Three different species of parasitoids were identified at the U.S. sites: *Diachasma alloeum* (80.1 ± 15.8% SD of all parasites across sites), *Utetes canaliculatus* (18.9 ± 15.1%), and *Diachasmimorpha mellea* (0.98 ± 1.6%).

Overall, parasitism levels were significantly lower for hawthorn flies in the SMO region of Mexico than in the United States (Table 2). In the SMO, a total of 11,889 *R. pomonella* pupae were recovered from the early fruiting hawthorns *C. rosei parrayana, C. rosei rosei, C. gracilor, C. greggiana, C. cuprina,* and late-fruiting *C. mexicana* across 30 sites. From these pupae, 6,314 flies and 369 adult parasitoids eclosed, resulting in an overall 5.52% parasitism rate. Parasitism rates varied widely among SMO sites. No parasitoids were detected at 14 of the 30 (46%) sites in the SMO. Parasitism levels at the 16 sites where wasps were present, ranged from 1.3% in La Joya, Veracruz, up to 25% in Achocoatlán, Hidalgo, al-

though there were relatively few flies and parasitoids reared from the latter site (mean parasitism rate for SMO populations that were parasitized = 10.8 ± 7.8% [SD]). Seven different parasitoid species were recovered from the SMO region: *U. canaliculatus* (77.2 ± 32.3% of all parasites averaged across sites), *Doryctobracon areolatus* (14.0 ± 5.0%), *Opius* sp. (13.9 ± 5.1%), *Utetes anastrephae* (13.9 ± 5.1%), *Diachasmimorpha mellea* (8.6 ± 2.4%), *Diachasmimorpha longicaudata* (6.4 ± 1.7), and *Aganaspis pelleranoi* (3.7 ± 12.9%).

In the EVTM region of Mexico, parasitism was extremely low (Table 2). Of a total of 17,432 *R. pomonella* pupae recovered from two species of late fruiting hawthorns, *C. rosei rosei* and *C. mexicana*, across 30 EVTM sites, 7,659 flies and only 15 adult parasitoids emerged (0.19% overall parasitism rate). Parasitoids were totally absent in 24 of the 30 EVTM sites (80%). In the six EVTM sites where parasitoids were present, parasitism rates were low, ranging from 0.17% in the Distrito Federal up to 4.3% in San Martín, Puebla. The mean parasitism rate for the six EVTM populations where parasitoids were present was 1.9 ± 1.5%. Five parasitoid species were recovered in the EVTM region: *Diachasmimorpha mexicana* (40.0 ± 54.7% across sites of all parasitoids), *Diachasmimorpha longicaudata* (20.0 ± 44.7%), *Doryctobracon areolatus* (20.0 ± 44.7%), *Utetes anastrephae* (15.0 ± 33.5%), and *U. nr. canaliculatus* (5.0 ± 11.18%).

Parasitism rates were also exceedingly low in the Chiapas highlands of Mexico (Table 2). Of a total of 5,560 *R. pomonella* (or near *pomonella*) pupae recovered from *C. mexicana* fruit at one site in Chiapas, 2,671 flies and only 4 adult parasitoids emerged (0.14% overall parasitism rate). Parasitoid diversity was limited in the Chiapas highlands, because the only species recovered was an undescribed *Opius* closely resembling *U. canaliculatus.*

All species of parasitoids recovered from hawthorn infesting *Rhagoletis* were found to be solitary.

Parasitoid Diversity. Shannon-Weiner diversity indexes showed no significant differences in species

Table 2. Collecting site data for hawthorn species, *R. pomonella* flies, and parasitoid wasps sampled in the study

Host species	Locality	Date	Pupae	Flies	Parasitoids	Parasitism (%)	Species composition
Midwestwern United States							
Crataegus mollis (Torr. and A.Gray) Scheele	Grant, MI	15 Sept. 2004	661	307	153	33.3%	*Diachasma alloeum* 75.2% *Utetes canaliculatus* 24.8%
	Casnovia, MI	2003	500	211	59	21.8%	*Diachasma alloeum* 74.1% *Utetes canaliculatus* 22.2% *Diachasmimorpha mellea* 3.7%
	Fennville, MI	2003	ND	331	248	42.8%	*Diachasma alloeum* 59.7% *Utetes canaliculatus* 39.1% *Diachasmimorpha mellea* 1.2%
	Granger, IN	2003	ND	149	8	5.1%	*Diachasma alloeum* 100%
	South Bend, IN	17 Oct. 2005	582	412	58	12.2%	*Diachasma alloeum* 91.4% *Utetes canaliculatus* 8.6%
Sierra Madre Oriental							
Crataegus mexicana Moc. and Sessé	Puebla: Xoxonacaxtla	13 Sept. 2004	449	208	67	24.4%	*Utetes* near *canaliculatus* 95.5% *Opius* sp. 1.5% *Diachasmimorpha mellea* 3%
	Veracruz: La Joya	22 Aug. 1996	ND	ND	1	N.D	*Utetes* near *canaliculatus* 1
		1999	ND	ND	3	N.D	*Utetes* near *canaliculatus* 3
		14 Sept. 2002	603	299	4	1.3%	*Aganaspis pelleranoi* 50% *Doryctobracon areolatus* 25% *Utetes* near *canaliculatus* 25%
	Las Vigas	9 Sept. 2001	320	212	0		
		10 Sept. 2002	909	526	0		
		15 Oct. 2003	27	14	0		
		4 Nov. 2003	31	3	0		
		15 Nov. 2001	50	29	0		
Crataegus gracilor J. B. Phipps	Hidalgo: Acoalitlán	10 Sept. 2003	5	2	0		
	Los Duraznos	23 Sept. 2004	128	58	5	7.9%	*Utetes* near *canaliculatus* 100%
	La Mojonera	26 Sept. 2004	154	82	4	4.6%	*Utetes* near *canaliculatus* 75% *Opius* sp. 25%
	La Mora	24 Sept. 2004	207	86	0		
	Querétaro: Santa Ana	20 Sept. 2003	67	17	3	15%	*Utetes* near *canaliculatus* 100%
	Puebla: Chingnahuapan	15 Sept. 2004	78	70	8	10.2%	*Utetes* near *canaliculatus* 100%
	Veracruz: Rafael Lucio	25 July 2002	164	83	2	2.3%	*Utetes* near *canaliculatus* 100%
		24 Sept. 2002	26	13			0
Crataegus rosei Eggl. subsp. *parrayana*	Hidalgo: Achocoatlán	18 Sept. 2003	31	12	4	25%	*Utetes anastrephae* 25% *Diachasmimorpha longicaudata* 25% *Doryctobracon areolatus* 50%
	Durango	24 Sept. 2004	79	7	1	12.5%	*Utetes* near *canaliculatus* 100%
	La Pechuga	25 Sept. 2004	94	76	0		
	Zoquiazoquitlán	26 Sept. 2004	73	22	5	18.5%	*Utetes* near *canaliculatus* 100%
	Puebla: Miradores	12 Sept. 2004	124	34			0
	Poxcuatzingo	14 Sept. 2004	80	21			0
	Querétaro: San Joaquín	24 Sept. 2001	344	138	2	1.4%	*Utetes* near *canaliculatus* 50% *Utetes anastrephae* 50%
	San Luis Potosí: Carretera a Rio Verde	7 Oct. 2003	47	21	2	8.7%	*U.* near *canaliculatus* 50% *Opius undsc* 50%
	Valle de los Fantasmas	6 Oct. 2003	27	4	0		
	Veracruz: El Rosario	25 July 2002	178	127	0		
	Piletas	27 July 2001	1,126	180	0		
Crataegus rosei Eggl. subsp. *rosei*	Hidalgo: Ixmiquilpan (Lagunita-La Pechuga)	19 Sept. 2002	4,307	2,859	209	6.8%	*U. anastrephae* 1.4% *U.* near *canaliculatus* 96.6% *D. longicaudata* 1% *D. areolatus* 0.5% *Aganaspis pelleranoi* 0.5%
		2005		1,048	45	4.1%	*Utetes* near *canaliculatus* 100%
	Minas Viejas	23 Sept. 2004	22	4	0		
	La Mora	24 Sept. 2004	6	2	0		
	Nuevo León: Santiago	19 Oct. 2002	68	19	0		
	San Luis Potosí: San Francisco	7 Oct. 2003	45	14	3	17.6%	*Utetes* near *canaliculatus* 66.6% *D. mellea* 33.3%

Table 2. Continued

Host species	Locality	Date	Pupae	Flies	Parasitoids	Parasitism (%)	Species composition
Crataegus spp.	Hidalgo: Molango	31 Oct. 2003			1		
	Nuevo Leon: Cerro el Potosí	3 Oct. 2003			1		*Utetes anastrephae* 1
	Veracruz: La Joya	22 Aug. 1996	ND	ND	0		
Crataegus greggiana Eggl.	Coahuila: El Tejocote	6 Oct. 2003	24	16	0		
Crataegus cuprina J. B. Phipps	Nuevo León: El Orito	5 Oct. 2003	19	8	0		
Eje Volcánico Trans Mexicano							
Crataegus mexicana Moc. and Sessé	Distrito Federal (Tlálpan)	4 Nov. 2001	277	64	2	3%	*Diachasmimorpha longicaudata* 100%
		13 Nov. 2001	120	50	0		
		17 Oct. 2002	4,255	2,743	0		
		04 Nov. 2002	2,779	829	0		
		23 Oct. 2003	3,206	2,200	0		
		2005	ND	575	1	0.17%	Lost specimen 100%
	Guerrero Peral Tetipac	22 Nov. 2003	25	11	0		
	Hidalgo: Atotonilco	4 Nov. 2002	280	54	1	1.8%	*Diachasmimorpha mexicana* 100%
	Jalisco: Atemajac de Brizuela	4 Nov. 2004	129	15	0		
	Los Garcia	5 Nov. 2004		27	0		
	Mazmitla	5 Nov. 2004	62	1	0		
	Tapalpa	5 Nov. 2004	228	27	0		
	México: Texcoco	17 Oct. 2001	153	3	0		
	Atlacomulco	6 Nov. 2004	7	1	0		
	Carretera Zitácuaro	1 Nov. 2004	204	3	0		
	Toluca	6 Nov. 2004	646	163	0		
	Valle de Bravo	1 Nov. 2004	147	18	0		
	Michoacán: Tancítaro	8 Oct. 2001	184	510	4	0.8%	*Utetes* near *canaliculatus* 25% *Utetes anastrephae* 75%
		5 Nov. 2001	697				
		19 Nov. 2001	80				
		2 Dec. 2001	370				
		19 Dec. 2001	49				
	Angangueo	1 Nov. 2004	218	61	0		
	Ciudad Hidalgo	1 Nov. 2004	428	12	0		
	La Dieta	1 Nov. 2004	350	55	0		
	Mil Cumbres	1 Nov. 2004	129	44	0		
	Uruapan	11 Sept. 2004	15	5	0		
	Villa Morelos	2 Nov. 2004	101	31	0		
	Morelos: Coajomulco	13 Nov. 2001	1,082	270	4	1.4%	*Doryctobracon areolatus* 100%
		16 Nov. 2002	585	347	0		
		2 Dec. 2004	85	15	0		
	Tres Marías	2 Dec. 2004	5	4	0		
	Puebla: San Martín Zacatempan	24 Nov. 2003	169	67	3	4.3%	*Diachasmimorpha mexicana* 100%
	Tlaxcala: Xaltocan	4 Nov. 2002	41	11	0		
Crataegus rosei Eggl. subsp. *rosei*	Michoacán: Tancítaro	23 Oct. 2001	326	18	0		
Chiapas							
Crataegus mexicana Moc. and Sessé	Chiapas: Teopisca	26 Nov. 2001	ND	ND	2	ND	*Opius undsc* 2
	San Cristóbal de las Casas	14 Nov. 2001	ND	ND	2	ND	*Opius undsc* 2
	Rancho Nuevo, Huixtán	15 Nov. 2002	5,193	2,671	4	0.14%	*Opius undsc* 100%

Percent parasitism was calculated by dividing the no. of emerged parasitoids by the total no. of emerged flies plus the total no. of parasitoids.

richness among geographical regions ($F_{2,25} = 1.2140$, $P = 0.31394$). The latter is explained by the fact that, in this index, the species/number relationship is dominated by the abundant species and index values go down when species become unevenly distributed in a region. In contrast, rarefaction curves showed greater species accumulation in the Sierra Madre Oriental than in the Eje Volcánico Trans Mexicano and the United States (Fig. 3).

Parasitoid Emergence Schedules. Parasitoid emergence times were significantly different among regions ($F_{2,80} = 227,42$, $P < 0001$) with emergence times increasing with decreasing latitude across the United States and Mexico, closely mirroring regional patterns (also significantly different among regions) of fly emergence ($F_{2,1698} = 4510,0$, $P < 0001$). At the Grant, MI, site in the United States, *R. pomonella* emerged an average of 63.3 ± 8.75 d ($n = 307$) after removal from the cold (Fig. 4A). The two most common parasitoids recovered from pupae at the Grant site, *D. alloeum* and *U. canaliculatus*, emerged a mean of 98.5 ± 11.2 ($n = 115$) and $90.5 \pm$
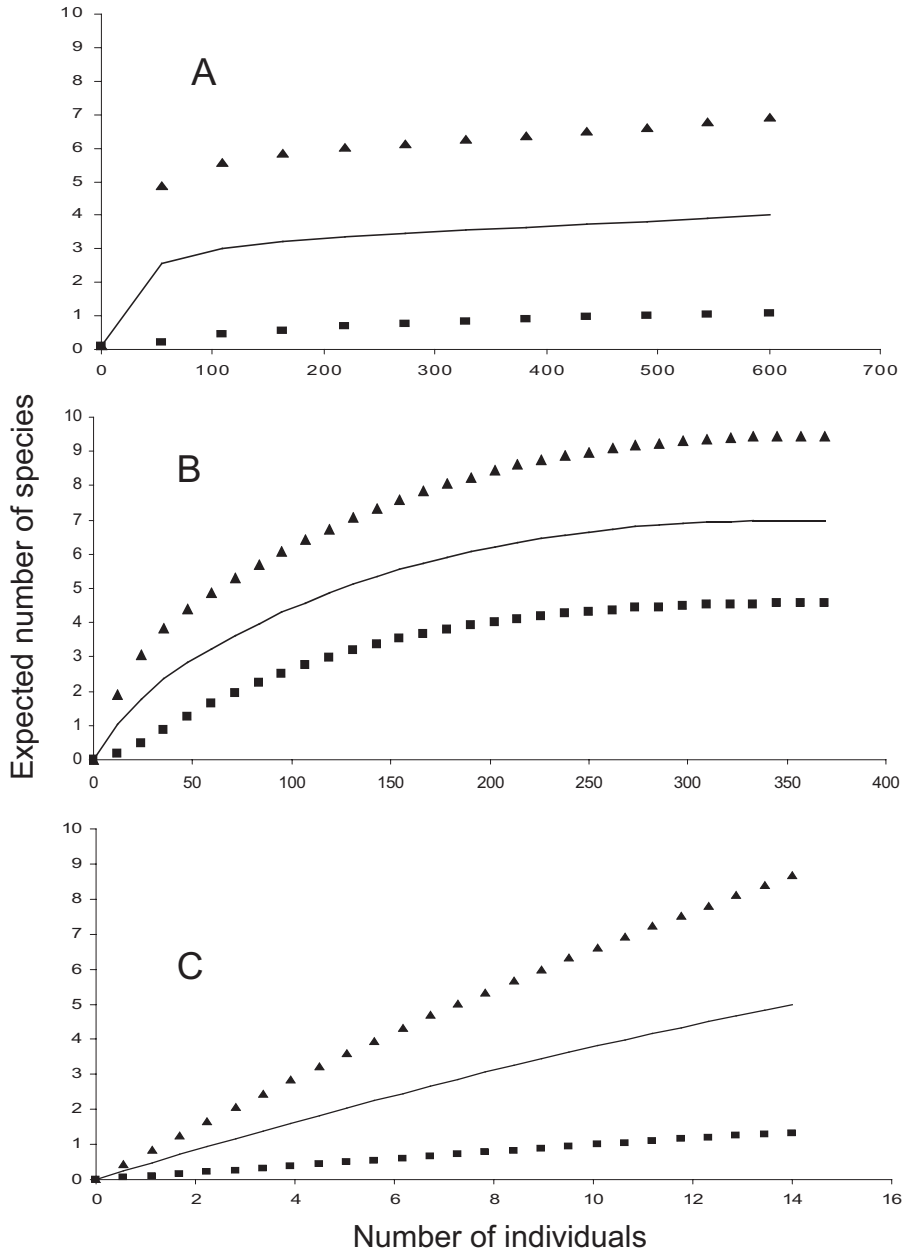
Fig. 3. Species accumulation curves (solid lines) and 95% confidence intervals (dotted lines) for parasitoids of hawthorn-infesting *Rhagoletis* in (A) midwestern and northeastern United States, (B) the Sierra Madre Oriental, Mexico, and (C) Eje Volcánico Trans Mexicano, Mexico.

9.07 d ($n = 38$), respectively, after exposure to ambient temperature after the simulated winter. Both hawthorn flies (114.3 ± 8.91 d, $n = 1,048$) and the parasitoid *U. canaliculatus* (133.7 ± 10.19 d, $n = 45$) emerged even later from the Ixmiquilpan site in the SMO than in Grant, MI (Fig. 4B). Finally, *R. pomonella* (142.7 ± 15.7 d, $n = 575$) and the single *U. canaliculatus* individual (182 d) that emerged from the Distrito Federal site in the EVTM did so the latest compared with all other sites (Fig. 4C).

Discussion

Four major findings emerged from our study. First, parasitism rates generally decreased, with decreasing latitude from an overall mean of 27.2% in the United States, to 5.49% in the SMO, to 0.19 and 0.14% in the EVTM and Chiapas highlands, respectively. Second, in terms of parasitism rate, parasitism was dominated across the *R. pomonella* range by two specialized species (*U. canaliculatus* and *D. alloeum*). Third, the life
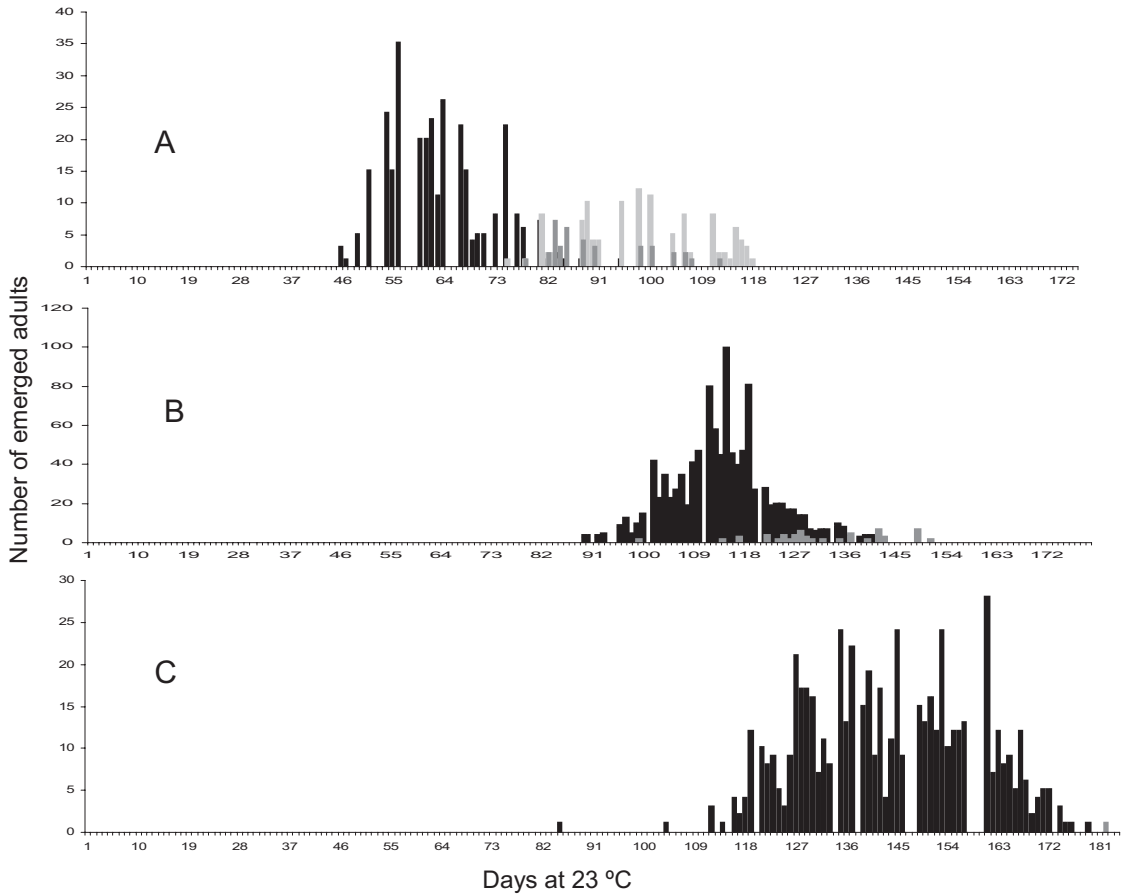
Fig. 4. Emergence schedules for flies (black) and associated parasitoids *U. canaliculatus* (dark gray) and *D. alloeum* (light gray) from (A) South Bend, IN, (B) Ixmiquilpan, SMO, Mexico, and (C) Distrito Federal, EVTM, Mexico.

histories of flies and wide-ranging dominant parasitoid species were closely synchronized across their distributions through the United States and Mexico, with time to emergence increasing with decreasing latitude. Fourth, species diversity in terms of parasitoid species recovered from fly samples was greatest in areas of greatest overlap (SMO) between temperate (*Rhagoletis*) and subtropical (*Anastrepha*) fly species, where generalist subtropical parasitoids occasionally used *Rhagoletis* as alternate hosts. However, subtropical parasitoid species populations were unable to build up on *Rhagoletis.*

We believe that the patterns described above may be inter-related. Environmental conditions, especially rainfall, can be more variable in Mexico than in the United States. In our study, the EVTM represents the driest region experiencing the widest fluctuation in annual precipitation, followed by the gulf-facing slope of the SMO. In contrast, the midwestern U.S. states of Michigan and Indiana represent a relatively humid region with a well-defined warm season. As a result, hawthorn fruit tend to be much more temporally and spatially patchy in the highlands of Mexico than in the midwestern United States. This interseasonal variabil-

ity in fruit resource can make fly abundance unpredictable, making it difficult for parasitoids to time and track local host populations. Moreover, the effects of environmental variability may be accentuated in Mexico by the delayed emergence times of both flies and parasitoids, increasing pupal mortality rates and further destabilizing parasitoid population dynamics causing perhaps a high frequency of local extinctions. We would like to highlight the fact that a recent study dealing with caterpillar-parasitoid interactions encompassing 15 collection sites for macro Lepidoptera also showed a decrease in parasitism as climatic variability, especially related to precipitation, increased across sites from Canada to Central Brazil (Stireman et al. 2005). We may be observing a similar pattern for *R. pomonella* along its distribution range.

Despite the differences in parasitism rates observed across the Unites States and Mexico, Shannon-Weiner diversity indexes failed to show differences in diversity of parasitoids emerging from hawthorn infesting *Rhagoletis.* We believe that such result reflects from the fact that parasitism, in terms of recovered individuals per species, is dominated by two species in the United States and one in Mexico. *Rhagoletis* popula-

tions in the United States and Mexico share *U. canaliculatus* and *D. mellea.* Only *U. canaliculatus* occurs over the entire *R. pomonella* range, accounting for the bulk of parasitism in the SMO (77.2%).

The remaining Mexican species, which account for greater species accumulation in the SMO, are not *R. pomonella* specialists, exhibiting rather broad host ranges, including many *Anastrepha* spp. fruit flies in Mexico (López et al. 1999, Sivinski et al. 2001, Aluja et al. 2003). The variation in the composition of the parasitoid guilds in the United States and Mexico is interesting for three reasons. First, the subtropical parasitoids that share *R. pomonella* as a host with other tephritids in Mexico (*Aganaspis pelleranoi, Diachasmimorpha mexicana, Diachasmimorpha longicaudata, Dorycobracon aerolatus, Opius* sp., and *Utetes anastrephae*), do not seem to be able to move northward into the northern United States (some are found in Florida; Eitam et al. 2004). Second, *D. alloeum*, which is the most common parasitoid attacking *R. pomonella* in the north, is completely absent in Mexico (and with the exception of one record in Florida, it is absent in southeastern United States). Third, two parasitoid species, *U. canaliculatus* and *D. mellea,* seem to be widespread parasitoids of *R. pomonella* infesting hawthorns.

Rates of parasitism in Mexico from subtropical parasitoid species that share *R. pomonella* (or near *pomonella*) as a host are low compared with the levels reported attacking other tephritid belonging to the genus *Anastrepha* (up to 83.8% parasitism; López et al. 1999, Sivinski et al. 2001). This suggests that these parasitoids may be using *R. pomonella* as a secondary resource in areas where *Anastrepha* hosts such as *A. ludens* happen to overlap in their distribution with *R. pomonella*–infesting hawthorns. *Anastrepha* are multivoltine in Mexico, having two or more generations per year (Aluja 1994). It is therefore possible that the inability of the subtropical parasitoids to exploit northern univoltine *R. pomonella* populations reflects the inability of these parasitoid species to enter a pronounced diapause and effectively overwinter. Additionally, numbers of generalist subtropical parasitoid species in high elevation areas in Mexico may not be able to build up on *R. pomonella* larvae because of the fact that only *Anastrepha ludens* and *Anastrepha fraterculus* are found at elevations >800 m (Sivinski et al. 2000). Such alternate host scarcity may prevent populations to build up before attacking *Rhagoletis* and only a few individuals may be able to colonize and persist on such a host.

All braconid species that we recovered parasitizing *Rhagoletis* in the United States are highly specialized on members of the genus. *D. mellea* has only been reported from *R. pomonella* in New England, New York, Ohio, Florida, Arizona, and Washington. *D. alloeum* has been recovered from *R. pomonella* and *R. mendax,* in Canada, New England, the midwest, and Florida, and *U. canaliculatus* infests various species only in the genus *Rhagoletis* and is widespread in North America with the exception of the southwestern United States (Wharton 2007; http://hym-

enoptera.tamu.edu/paroffit/). In contrast, parasitoid species exclusively recovered in Mexico during our survey show a much wider host range (several genera within Tephritidae) and seem to be opportunistic on *Rhagoletis. D. longicaudata* is native to Australasia and has been recovered from various species in the genera *Bactrocera, Ceratitis, Anastrepha,* and *Rhagoletis* (García-Medel et al. 2007). *D. areolatus* ranges from Argentina to Mexico and Florida, infesting several species of *Anastrepha, Rhagoletotrypeta,* and *C. capitata* (Ovruski et al. 2000). *U. anastrephae* also ranges from Argentina to Mexico and Florida and has been recovered from several species of *Anastrepha* and *C. capitata. A. pelleranoi* has also been recovered from *Anastrepha, Rhagoletis turpiniae,* and *C. capitata* (Ovruski et al. 2000).

Although the low rates of parasitism of *R. pomonella* by subtropical parasitoids may be understandable, the reason for the absence of the common northern species *D. alloeum* in Mexico is less clear. One possible explanation is that *D. alloeum* has gone regionally extinct because of the greater environmental variability in Mexican versus U.S. sites. It is also conceivable that *D. alloeum* has been incapable of evolving the necessary extended postdiapause eclosion timing to attack *R. pomonella* infesting hawthorn in Mexico. Resolution of this issue requires further study.

The occurrence of *U. canaliculatus* and *D. mellea* throughout a significant part of *R. pomonella*'s range in the United States and Mexico raises the question of whether the wide distribution of these parasitoids is recent and continuous or whether these parasitoids have undergone the same pattern of historical isolation and divergence as their fly host (Feder et al. 2003, 2005). An answer to this question awaits future analysis of the genetic structure of parasitoid populations through North America. In contrast to *D. alloeum, U. canaliculatus* seems to have the capacity to use *R. pomonella* as a host throughout the fly's range. An important component of this capacity is the ability of the parasitoid to adapt its adult emergence time to track that of *R. pomonella* in response to variation in hawthorn fruiting phenology. As a result, both *R. pomonella* and *U. canaliculatus* show geographic variation in emergence time, with insects from southern sites emerging later than those from northern populations. This trend is most pronounced in the EVTM. Here, the endemic hawthorns have evolved a distinctive late fruiting phenology (late November to early January) to cope with xeric conditions, which is closely mirrored by the delayed emergence characteristics of flies and parasitoids in the region.

In summary, we now have a general understanding of the parasitoid guild attacking hawthorn-infesting populations of *R. pomonella* across most of the fly's range in North America. Parasitism is more intense to the north in the United States, moderate in the SMO, and relatively rare in the EVTM and Chiapas highlands (Maier 1981, Gut and Brunner 1994, Feder 1995). Hawthorn flies in Mexico may escape parasitism because of the reduced ability of certain parasitoids to track variation in host fruiting phenology. In addition,

more variable environmental conditions in Mexico, especially with respect to rainfall, may cause fluctuations in local fly population densities that preclude the build up of large parasitoid numbers. Despite this, several fly parasitoids found in Mexico are not present in the United States. However, these wasps seem to represent cases of subtropical parasitoids using *R. pomonella* as a secondary host and do not reach high densities on hawthorn flies. Nevertheless, *U. canaliculatus* and to some degree *D. mellea* have been able to cope with the challenges posed by hawthorns and *R. pomonella*, attacking the fly through much of its range. Therefore, these parasitoid species present an opportunity for future studies to test for a shared biogeography and co-evolution between fly and parasitoid across trophic levels.

Acknowledgments

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